Chapter 1
The Mathematics of Extinction Across Scales: From Populations to the Biosphere

Colin J. Carlson, Kevin R. Burgio, Tad A. Dallas, and Wayne M. Getz

Abstract The sixth mass extinction poses an unparalleled quantitative challenge to conservation biologists. Mathematicians and ecologists alike face the problem of developing models that can scale predictions of extinction rates from populations to the level of a species, or even to an entire ecosystem. We review some of the most basic stochastic and analytical methods of calculating extinction risk at different scales, including population viability analysis, stochastic metapopulation occupancy models, and the species area relationship. We also consider two extensions of theory: the possibility of evolutionary rescue from extinction in a changing environment, and the posthumous assignment of an extinction date from sighting records. In the case of the latter, we provide a new example using data on Spix's macaw, the "rarest bird in the world," to demonstrate the challenges associated with extinction date research.

Key words: Sixth mass extinction, species area relationship, sighting records, population viability analysis, mean time to extinction

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> It's easy to think that as a result of the extinction of the dodo, we are now sadder and wiser, but there's a lot of evidence to suggest that we are merely sadder and better informed.
>
> – Douglas Adams, *Last Chance to See*

1.1 Introduction

Every species, like every living organism, has a finite lifespan. From the origin of a species onward, every species changes and adapts to its environment. Some species exist longer than others, but all eventually face extinction (or are replaced by their descendants through evolution). Currently, there are approximately 8.7 million eukaryote species alone. But in the history of the Earth, it is estimated that there have been a daunting 4 billion species altogether, and at least 99 percent of them are now gone [79].

How long can a species exist? Of the species currently on Earth, some are deeply embedded in the geological record and have changed very little over the span of hundreds of millions of years, such as coelacanths and ginkgo trees. Most species persist for a few millions of years or more, and in periods of environmental stability, extinctions typically occur at a low and steady baseline rate. But at various points in the history of the Earth, extinction rates have suddenly accelerated for brief and eventful periods that biologists term *mass extinction events*. In 1982, based on the marine fossil record, David Raup and Jack Sepkoski [85] suggested that five of these mass extinctions happened over the past half billion years. In all five, more than half of all contemporary species disappeared [76], and each extinction was sufficiently drastic to be identified with the end of a geological era: the Ordovician 444 million years ago (*mya*), Devonian 375 mya, Permian 251 mya, Triassic 200 mya and Cretaceous 66 mya.

In recent years, ecologists have reached the consensus that the biosphere is currently experiencing, or at the very least entering, the sixth mass extinction [62]. Unlike the previous five, which were caused by planetary catastrophes and other changes in the abiotic environments, the sixth mass extinction is the undeniable product of human activities. While anthropogenic climate change is one of the most significant contributors, a number of other factors have exacerbated extinction rates, including habitat loss and fragmentation, biological invasions, urbanization, overharvesting, pollution, pests, and emerging diseases.

How does the sixth mass extinction scale up against the last five? The number of extinctions alone is an unhelpful metric, as species richness changes over time. A more convenient unit of measurement commonly used by scientists is the number of *extinctions per million species-years* (E/MSY). From a landmark study by Gerardo Ceballos and colleagues, we know that in the geological record, vertebrates normally go extinct at a rate of 2 E/MSY in the periods in-between mass extinctions. But since 1900, that rate is an astounding 53 times higher [20]. One study has suggested that the sixth mass extinction is comparable to other mass extinctions in E/MSY rates, meaning that with enough time, the geological definition of a mass

extinction (three quarters extinction) could be achieved in hundreds to thousands of years [7]. Or, to consider another metric: a 1970 study estimated that at a baseline, one species goes extinct per year [68], while a decade later that estimate was revised to just up to one species per hour [80]. Plants, insects, and even micro-organisms all face similarly catastrophic threats; and these across-the-board losses of biodiversity pose a threat to human survival that some argue could even threaten our own species with extinction.

The crisis of extinction is, for scientists, a crisis of prediction. While extinction is a natural part of ecosystem processes and of the history of the planet, the job of conservation biologists is to protect species that would otherwise be brought to an untimely and avoidable end. To do that, conservationists must sort and prioritize the 8.7 million eukaryotes (and even some prokaryotes) to assess which species face the greatest threat—and which can, and cannot, be saved by human intervention. Assessment is easiest at the finest scales: by marking and tracking all the individuals in a region, a population ecologist can make a statistically informed estimate of the probability of imminent extinction. Above the population level, assessment is much more challenging, requiring sophisticated (and complicated) metapopulation models that are typically data-intensive. If a species is rare enough and the data are "noisy," its extinction may seem uncertain even after the fact; but mathematical models can help assign a probability to the rediscovery of a species once thought extinct, and resolve when (and even why) a species has disappeared long after it is gone. Above the level of a single species, measuring extinction is an altogether different problem, requiring a different type of model to explain how biodiversity arises and is maintained over time. Each of these modeling approaches represents a different aspect of a connected problem, and we deal with each in turn in this chapter. The models we present are seminal and well-known, but extinction risk modeling is a dynamic and rapidly-growing field. Consequently, these models only present a handful of the many different approaches that link different temporal and spatial scales of extinction together.

Outline of the Chapter. We begin by discussing the basic mechanics of extinction as a demographic process at the population scale, including population viability analysis, with a case study on evolutionary rescue processes (Section 1.2). In Section 1.3, we progress up to the metapopulation scale, including patch occupancy models and island biogeography. At the species scale, we dive deeper into the issue of evolutionary rescue, including the potential for plasticity to buffer species from extinction in a changing environment (Section 1.4). Expanding at the species level, we discuss the recently-growing literature on using sighting records to determine the odds that species are extinct, with a handful of case studies including Spix's macaw and the ivory-billed woodpecker. In the final Section 1.5, we discuss how extinction scales up to the community level, and how extinction rates are inferred from habitat loss using macroecological theory.

1.2 The Population Scale

Even though many make a terminological distinction between *extinction* (the loss of a species) and *extirpation* (the eradication of a population), extinction is still fundamentally a process that begins at the population scale. With the exception of sudden, unexpected catastrophes, extinction at the population scale is almost always the product either of a declining population or of stochastic variations in an already small population, both of which follow mathematical rules that can be used to quantify extinction risk. Perhaps the most significant body of theory about population extinction deals with the estimation of a population's *mean time to extinction* (MTE, typically T_E in mathematical notation), an important quantity to both theoretical ecologists and to conservation efforts. For both theoretical and applied approaches to extinction, understanding the uncertainty around T_E requires an understanding of the shape of the extinction time distribution, including developing and testing demographic theory that accurately captures both the central tendencies [30] and the long tail [31] of empirical extinction times. We begin by reviewing some of the basic population-scale approaches that scale up to ecosystem-level theory of extinction.

1.2.1 Stochasticity and the Timing of Extinction

The simplest deterministic equation governing the size N of a population as it changes over time t (generally measured in units of either years or generations) is given by

$$\frac{dN}{dt} = rN. \tag{1.2.1}$$

The population is growing if $r > 0$, while the population heads towards extinction if $r < 0$. A slightly more complicated model that captures the phenomenological capping of the growth of a population at a *carrying capacity* K is

$$\frac{dN}{dt} = \begin{cases} rN & \text{if } 1 < N < K, \\ 0 & \text{if } N = K. \end{cases} \tag{1.2.2}$$

Equations (1.2.1) and (1.2.2) both imply that, if $r < 0$, $\ln(N)$ declines linearly with slope r. The mean time to extinction, T_E, for a shrinking population can be derived analytically as the amount of time before the population reaches one individual, $N(T_E)$=1,

$$T_E(N_0) = -\ln(N_0)/r. \tag{1.2.3}$$

Consequently, the maximum achievable extinction time for a given population with a fixed r, given a starting stable population size, would be

$$\max(T_E) = -\ln(K)/r. \tag{1.2.4}$$

But deterministic models only tell a part of the story. In the history of conservation biology, two paradigms emerged that separately explain the process of population extinctions. The *declining population paradigm* explains that populations shrink and vanish due to a combination of internal and external failures, and suggests that the key to conserving populations is to identify and prevent those failures. In contrast, the *small population paradigm* is rooted in ideas of stochasticity, suggesting that even without factors like environmental degradation or disease, smaller, more fragmented populations simply face higher extinction risk due to stochastic population processes [19]. For one thing, stochasticity produces populations with a log-normal distributed size (i.e., most populations are comparatively small relative to a few larger ones) due to Jensen's inequality, which can be applied to stochastic processes to show that if r is stochastic, the expectation $E[r]$ of r will always be greater than the expected real growth rate of the population [13],

$$E[r] > E[(N_t/N_0)^{1/t}]. \tag{1.2.5}$$

As a result, stochastic sub-exponential populations all tend eventually to extinction.

In reality, populations show a combination of deterministic and stochastic processes over time, and their extinction is a product of both. In the late 1980s, the field of *population viability analysis* (PVA) emerged from the need to find appropriate analytical and simulation methods for predicting population persistence over time. According to one history of PVA, Mark Shaffer's work on grizzly bears in Yellowstone [9] helped birth the field through two important developments, which we break down in turn below.

Demographic and Environmental Stochasticity. Shaffer's first major contribution was the use of extinction risk simulations that account for—and differentiate between—two major kinds of stochasticity, namely *demographic stochasticity*, which is defined at the scale of the individual and occurs through random variation in demography and reproduction, and *environmental stochasticity*, which occurs at a synchronized scale for an entire population (e.g., a bad year may change vital rates uniformly for all individuals in a population). While the impact of environmental stochasticity is ultimately scale-independent, larger populations become less sensitive to demographic stochasticity as they grow. This is due to the integer-based nature of birth and death processes, where populations made up of fewer individuals will suffer a disproportionate effect from a birth or death event.

Demographic and environmental stochasticity have measurably different effects on T_E in basic population models. A simple modeling framework distinguishing between them was laid out in a 1993 paper by Russell Lande [64]. That framework begins again with Eq. (1.2.2), except that we now regard r as an explicit function of time. In the case of demographic stochasticity, individual variations have no temporal autocorrelation, and at the population scale,

$$r(t) \sim \mathcal{N}(\bar{r}, \sigma_d^2/N), \tag{1.2.6}$$

where σ_d^2 is the variance of a single individual's fitness per unit time. Once again, for populations starting at their carrying capacity,

$$T_E = \left(\frac{1}{\bar{r}} \int_1^K \frac{e^{2r(N-1)/\sigma_d^2}}{N} \, dN \right) - \frac{\ln K}{\bar{r}}. \tag{1.2.7}$$

When $\bar{r} > 0$, MTE scales exponentially with carrying capacity, $T_E \propto e^{2r(N-1)/\sigma_d^2}/K$, while when $\bar{r} < 0$, it scales logarithmically, $T_E \propto \ln(K)$, much like in the deterministic decline given by Eqs. (1.2.3) and (1.2.4). In contrast, in the case of environmental stochasticity, the variance acts on the entire population at once,

$$E[\ln N(t)] = \ln N_0 + (\bar{r} - \sigma_e^2/2)\, t, \tag{1.2.8}$$

and the mean time to extinction is now given by

$$T_E = \frac{2}{V_e c} \left(\frac{K^c - 1}{c} - \ln K \right), \quad c = \frac{2\bar{r}}{\sigma_e^2} - 1. \tag{1.2.9}$$

In the case of environmental stochasticity, if the "long-run growth rate" ($\tilde{r} = \bar{r} - \sigma_e^2/2$) is zero or negative, MTE again scales logarithmically with K. When long-run growth is positive, the dynamic is a bit more complicated,

$$T_E \approx 2K^c/(\sigma_e^2 c^2) \quad \text{if} \quad c \ln K \gg 1. \tag{1.2.10}$$

In this case, the scaling of MTE with K curves up if and only if $\bar{r}/\sigma_e^2 > 1$ (i.e., if and only if the intrinsic growth rate exceeds environmental variation).

Minimum Viable Populations and Effective Population Size. The second major contribution of Shaffer's work was the introduction of the concept of a *minimum viable population* (MVP). In Shaffer's original work, MVP is defined as the smallest possible population for which there is a 95% chance of persistence (a 5% or lower chance of extinction) after 100 years. In their foundational treatment of the minimum viable population concept, Gilpin and Soulé [43] identify four special cases—*extinction vortices*—in which a population is likely to tend towards its MVP and ultimate extinction. The first, the *R Vortex*, is perhaps the most obvious: demographic stochasticity (variation in r) reduces populations and increases variation in r, a positive feedback loop of demographic stochasticity directly driving populations to extinction. The *D Vortex* occurs when the same processes—potentially in concert with external forces—produce increased landscape fragmentation (see Section 1.3.1 for an explanation of D), which not only reduces local population sizes (increasing local extinction rate) but also has subtle effects on population genetic diversity. The final two vortices—the *F Vortex* and *A Vortex*—both concern the genetic and evolutionary trajectories of small stochastic populations. In the former, inbreeding and demographic stochasticity form a feedback cycle, while in the latter, maladaptation is the underlying mechanism of extinction. Both are especially relevant in research

surrounding phenomena like climate change, but fully understanding them requires a mathematical language for the genetic behavior of near-extinction populations.

In heavily subdivided populations with low dispersal, increased inbreeding can lead to decreased genetic diversity and the accumulation of deleterious or maladapted alleles that make the total population less viable than its size might indicate. As a consequence, intermediate-size populations with low genetic diversity can behave, mathematically, like small populations. *Effective population size*, N_e, quantifies that phenomenon, expressing the genetically or reproductively "effective" number of individuals in a population. In some cases, measuring population size with N_e may more readily allow the computation of a meaningful and predictive MVP, by removing some of the variability between different populations of the same size and by more accurately capturing the long-term reproductive potential of the available genetic material. (Relatedly, it is worth noting that in one unusual study, it was found that there is no statistical link between species MVP and global conservation status [15].)

A number of different approaches exist for the estimation of N_e. Sewall Wright, who created the concept of effective population size, offered one interpretation based on neighborhoods. In his model, offspring move a distance away from their parent based on a two-dimensional spatial normal distribution with standard deviation σ [108]. If individuals have a density D, then

$$N_e = 4\pi\sigma^2 D. \tag{1.2.11}$$

Wright [109] also provides a more commonly invoked method of calculating N_e based on sex structure, using N_m and N_f to respectively denote the number of breeding females and males in the population,

$$N_e = \frac{4N_m N_f}{N_m + N_f} \tag{1.2.12}$$

In such an approach, a population of all males or all females would have $N_e = 0$ because no new offspring could be produced in the next generation, rendering the population functionally extinct. That method of deriving N_e is still frequently cited in population conservation work, as small populations tend to stochastically deviate from a 50:50 sex ratio, sometimes severely impacting long-term survival.

A more genetics-based method of calculating N_e comes from the Wright–Fisher model of a two-allele one-locus system, referred to as the *variance effective population size* [21]. In that model, variance between generations $\sigma^2(a)$ for allele A with frequency a is given as $a(1-a)/(2N)$, resulting in an effective population size

$$N_e = \frac{a(1-a)}{2\sigma^2}. \tag{1.2.13}$$

Alternatively, for a locus with a greater degree of polymorphism, or multi-locus microsatellite data, genetic diversity θ and mutation rate μ are related by

$$N_e = \frac{\theta}{4\mu}. \tag{1.2.14}$$

A more commonly used metric in current literature is *inbreeding effective population size*. To construct that metric, we start by defining population-level measures of heterozygosity. In the simplest Hardy–Weinberg formulation for a two-allele system with allele frequencies a and $1-a$, the expected fraction of heterozygote offspring is $E(H) = 2a(1-a)$. By counting the real fraction of heterozygotes and comparing, we can measure the assortiveness of mating,

$$f = \frac{E(H) - H}{H}. \tag{1.2.15}$$

That value f is called the inbreeding coefficient, ranging from 0 to 1; again according to Wright [3], N_e should be calculated such that it satisfies

$$N_e = \frac{1}{2\Delta f}, \tag{1.2.16}$$

where Δf is the change per generation (in a declining or small population, genetic diversity decreases at a rate determined by the population size and inbreeding).

Returning to the extinction vortex concept with N_e in mind clarifies the genetic component of those extinction processes. While the *D Vortex* reduces N_e as a byproduct of fragmentation (in fact, decreasing neighborhood size), the last two extinction vortices bring N_e below the MVP through specifically genetic modes of extinction. In the *F Vortex*, a positive feedback loop between increased inbreeding (hence f, the inbreeding coefficient) and decreases in effective population size drive a population to extinction over a few generations. A notorious real-world example of such a process might be the near-extinction (or extinction, depending on one's species concept) of the Florida panther, a subspecies of *Puma concolor* ultimately rescued through outbreeding with Texas panthers. All things considered, their rescue was both fortuitous and improbable, as the species was assigned a 5% or less chance of avoiding imminent extinction in 1995 [56]. Finally, in the *A Vortex* (for adaptation), decreased N_e acts as a buffer to the strength of selection acting on phenotypes that are closely paired with environmental variation or change, leading to mismatch between them that reduces both r and N (and N_e) until extinction (a process we cover in much greater detail in Section 1.4.1) . Obviously, the four vortices are not independent processes and probably often exist in combination in real-world cases of population extinction.

Population Viability Analysis through Simulation. Usually, MVP is often calculated through simulation methods, which benefit from a greater ease of incorporating age, sex structure and other population-scale heterogeneities. Even though these methods are still the foundation of most population-level extinction analyses, they date as far back as P. H. Leslie's population analyses in the late 1940s in the framework of discrete matrix models and linear systems theory. Formulations of the

Leslie model and the theory behind such models can be found in several expository texts [18, 40], with a brief outline provided here.

In the Leslie model, the population is divided into n age classes, where $N_i(t)$ is used to denote the number of individuals in age class i at time t. In each age class, the parameter s_i $(0 < s_i \leq 1)$ is used to represent the proportion of individuals aged i that survive to age $i+1$, in which case the variables $N_i(t)$ and $N_{i+1}(t+1)$ are linked by the equation

$$N_{i+1}(t+1) = s_i N_i(t). \tag{1.2.17}$$

We either terminate this sequence of equations at age n by assuming that $s_n = 0$ (i.e., no individuals survive beyond age n), or we interpret N_n as the group of individuals in the population aged n and older and use the equation

$$N_n(t+1) = s_{n-1}N_{n-1}(t) + s_n N_n(t) \tag{1.2.18}$$

to imply that all individuals aged n and older are subject to the survival parameter s_n (i.e., individuals older than age n are indistinguishable from individuals aged n). If we now interpret $N_0(t)$ as all newborn individuals born just after individuals have progressed one age class, then $N_0(t)$ can calculated using the formula

$$N_0(t) = \sum_{i=1}^{n} b_i N_i(t), \tag{1.2.19}$$

where b_i is the average (expected) number of progeny produced by each individual aged i. In this model we have not differentiated between the sexes; so, for example, if each female aged i is expected to produce three young and the population has a 1:1 sex ratio (same number of males to females), then $b_i = 1.5$ for this age class. If we now apply Eq. (1.2.17) for the case $i = 0$, we obtain the equation

$$N_1(t+1) = s_0 N_0(t) = s_0 \sum_{i=1}^{n} b_i N_i(t). \tag{1.2.20}$$

Equations (1.2.17)–(1.2.20) can be written compactly in matrix notation,

$$\mathbf{N}(t+1) = L\mathbf{N}(t), \tag{1.2.21}$$

where

$$\mathbf{N} = \begin{pmatrix} N_1 \\ \vdots \\ N_n \end{pmatrix}, \quad L = \begin{pmatrix} s_0 b_1 & \cdots & s_0 b_{n-1} & s_0 b_n \\ s_1 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & s_{n-1} & s_n \end{pmatrix}.$$

The *Leslie matrix* L is nonnegative, since all its elements are nonnegative, with at least one positive element. Further, if there exists some integer $p > 0$ such that L^p is positive (i.e., all its elements are positive), then it is is known by the *Perron–Frobenius Theorem* that the matrix L has a dominant positive eigenvalue λ_p (known as the *Perron root*) and a corresponding eigenvector $\mathbf{v}_p$ whose elements are all pos-

itive; λ_p and $\mathbf{v}_p$ characterize the long-term behavior of $\mathbf{N}$,

$$\mathbf{N}(t) \sim (\lambda_p)^t \mathbf{v}_p. \tag{1.2.22}$$

That is, $\mathbf{N}(t)$ grows like $(\lambda_p)^t$ as t gets very large, and the ratio of different age classes matches the ratio of elements of $\mathbf{v}_p$. This implies that, if $\lambda_p > 1$ ($\lambda_p < 1$), $\mathbf{N}(t)$ will grow (decline) geometrically as λ_p^t and approach the *stable age-distribution* characterized by the ratio of consecutive elements of $\mathbf{v}_p$. Thus, this model predicts that the population will go extinct whenever the largest eigenvalue of L is less than one ($0 < \lambda_p < 1$). On the other hand, if $\lambda_p > 1$, then we expect density-dependent effects at some point to rein in the unfettered growth by causing survival rates to decline. In particular, if the survival rate s_0 of the youngest age class is the most dependent of all the survival rates on the total biomass density $B = \sum_1^n w_i N_i$, where $w_i > 0$ is the average weight of an individual in age class i, then we should replace s_0 in Eqn. (1.2.20) with an expression such as

$$s_0 = \frac{\hat{s_0}}{1 + (B/K_0)^\gamma}, \tag{1.2.23}$$

where $\hat{s_0}$ is the density-independent survival rate, K_0 is the density at which $\hat{s_0}$ is halved, and $\gamma > 1$ is a so-called abruptness parameter (which controls the abruptness in the onset of density, approaching a step down function as γ gets large [39]). Similar modifications can be made to the other survival parameters s_i, depending on their sensitivity to changes in population density.

Stochastic equivalents of these deterministic models typically treat the survival rates s_i as probabilities that each individual survives each time period, rather than as the proportion of individuals surviving each time period; and b_i itself is a random variable drawn from an appropriately defined distribution (usually the binomial distribution). Stochastic models of this sort can be made even more complex by adding more population structure (e.g., genetic variability) or increased levels of complexity (e.g., modeling at the metapopulation scale, discussed in Section 1.3, or adding underlying environmental variation or other landscape structures). Though MVP or extinction rates might be difficult to calculate analytically for models of this level of complexity, repeated simulation can easily allow empirical derivation of these properties of a system [77] and is perhaps the most widespread practice for estimating population extinction risk in conservation research. An example using an interactive web app [41] is shown in Figure 1.2.1.

1.2.2 Case Study: PVA, Disease, and Evolutionary Rescue

In 2015, an epidemic of unknown identity eliminated more than half of the population of the critically endangered saiga antelope (*Saiga tatarica*) in the short span of three weeks. While the causative agent was ultimately identified as a species of *Pasteurella*, the mechanism by which a normally asymptomatic non-pathogenic bac-

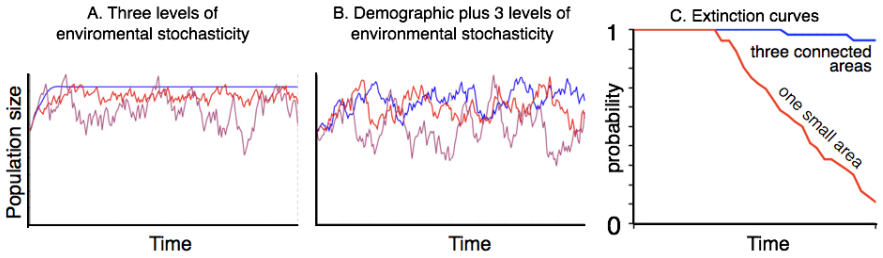

Fig. 1.2.1: An example PVA without (A) and with (B) demographic stochasticity, with no (blue), medium (red) and high (purple) environmental stochasticity. With repeated simulation, an "extinction curve" can be plotted from the probability of population survival over time (C). The analysis can be used to make decisions about management and conservation: here, illustrating that three populations with migration between them survive much longer in a poached population of rhinos than a single population. An interactive tutorial of PVA, which can be adjusted to produce anything from the simplest population dynamics to a stochastic, structured metapopulation experiencing harvesting can be found at `http://www.numerusinc.com/webapps/pva`.

terium killed at least 130,000 antelopes is still in question [78]. Literature explaining the die-off, or predicting the consequences for the species, remains comparatively limited; the fate of the species remains uncertain, and it may yet face extinction in the coming years.

Disease is rarely responsible for the extinction of a cosmopolitan species. But for already-threatened species like the saiga, it can be one of the most rapid, unpredictable and unpreventable mechanisms of extinction. Disease has been implicated in a handful of notable wildlife extinctions, like that of the thylacine (*Thylacinus cynocephalus*) or Carolina parakeet (*Conuropsis carolinensis*), and has been the definitive mechanism of extinction for species like the eelgrass limpet (*Lottia alveus*). [26] While most diseases co-evolve with their hosts to an optimal virulence that prevents the species from reaching extinction, diseases that can persist in the environment may be released from such constraints and be more likely to evolve "obligate killer" strategies (like that of anthrax [38]). Fungal pathogens in particularly tend to have rapid intra-host growth rates and high transmission potential, which can result in population collapses before optimal virulence levels can be attained [36].

Two notable fungal diseases have recently demonstrated the destructive potential of environmentally transmitted pathogens. Perhaps the most significant example of disease-driven extinctions is the trail of destruction caused by the chytrid fungus *Batrachochytrium dendrobatidis* (Bd). Bd has been found in at least 516 species of amphibians [81] and has driven decline or extinction in at least 200 [97], including at least two-thirds of the genus *Atelopus* alone [83]. According to some estimates, current extinction rates that amphibians face (largely but not entirely due to chytrid)

are roughly 200 times the background rate; including declining species, that estimate is closer to an even more staggering 25-45,000 [74]. White-nose syndrome (*Geomyces destructans*), a similar fungal epizootic, has similarly spread through bat populations in the eastern United States, causing widespread population-level die-offs since the mid-2000s. While white-nose syndrome has yet to drive any entire species to extinction, significant concern remains regarding its ongoing spread; one study in 2010 using population viability analysis suggested a 99% extinction risk for the little brown bat *Myotis lucifugus* in under two decades. Even in a best-case scenario where white-nose mortality was reduced to one-twentieth of its rate, substantially reducing extinction risk, bats would still be reduced to one percent of their original population size.

White-nose syndrome (WNS) has also become a potential case study for evolutionary rescue, one of the most controversial phenomena in extinction research. The premise that rare genes for resistance or tolerance can bring a disease-ridden population back from the brink of extinction has theoretical support, and potentially indicated from the rapid evolutionary response of certain hosts documented throughout the literature [4]. But WNS constitutes one of the most interesting and controversial examples because, while populations show some sign of recovery from the disease at the time of this writing, no definitive genetic mechanism for resistance has been isolated—a necessary component of demonstrating evolutionary rescue from disease-induced extinction [4]. Consequently, speculation about evolutionary rescue is controversial and so far has been conducted in primarily theoretical settings. In an age-structured matrix population model proposed by Maslo and Fefferman, two scenarios for recovery from WNS are considered [72]. In one model, bats' adaptive immunity leads to re-stabilization at much lower levels overall, but a much faster recovery to a stable balance of juveniles (J) and adults (A), with subscript t denoting the number of individuals in these two age classes at time t. In that model, in the absence of WNS,

$$\begin{pmatrix} J_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} 0.95 & 0.35 \\ 0.95 & 0.87 \end{pmatrix} \begin{pmatrix} J_t \\ A_t \end{pmatrix}. \tag{1.2.24}$$

In a second model, recovery comes not from adaptive immunity but from innate immunity through a genetic mechanism for resistance. In that scenario, a robust type (R) is present in the gene pool with frequency p and the remainder of individuals are wild type (WT), resulting in the matrix model

$$\begin{pmatrix} J_{t+1} \\ A_{t+1} \end{pmatrix} = p_t \begin{pmatrix} 0.86 & 0.32 \\ 0.86 & 0.78 \end{pmatrix} \begin{pmatrix} J_t^{\mathrm{R}} \\ A_t^{\mathrm{R}} \end{pmatrix} + (1-p_t) \begin{pmatrix} 0.52 & 0.27 \\ 0.52 & 0.46 \end{pmatrix} \begin{pmatrix} J_t^{\mathrm{WT}} \\ A_t^{\mathrm{WT}} \end{pmatrix}. \tag{1.2.25}$$

In this model, an 11-year stabilization period ultimately leads to population recovery with a positive net growth rate (calculated as the dominant eigenvalue $\lambda = 1.05$), potentially saving populations from extinction. Despite the lack of genetic evidence for evolutionary rescue, Maslo and Fefferman propose that observed similarities between the dynamics they observe and real data on white-nose outbreaks suggests that evolutionary rescue may be happening in real time.

1.3 The Metapopulation Scale

Populations rarely exist in isolation, but are often connected to other populations through dispersal processes, creating a metapopulation. Metapopulations are considered to be in a relatively constant state of flux, as local extinctions of species in habitat patches are buffered by recolonization by dispersal. In this way, dispersal can be beneficial or detrimental to metapopulation persistence. Under high dispersal, patches become homogeneous and population dynamics tend to become synchronous. This synchrony is destabilizing, in that periods of low population sizes will be experienced by all patches, increasing the likelihood of stochastic extinction of the entire metapopulation. On the other hand, too little dispersal will result in spatial clustering of a species, as the species will be confined to the set of patches that can be successfully reached and colonized and similarly potentially increasing extinction risk [1, 2].

The importance of dispersal to patch-level colonization and metapopulation persistence highlights that extinction processes occur at two scales in metapopulations. Specifically, extinction can occur both at the local patch-level (i.e., a single population in the network of habitat patches) or at the entire metapopulation level (i.e., either through catastrophic events or cascading local extinctions). Extinctions of single patches can occur as a result of demographic, environmental, or genetic stochasticity (addressed in more detail in Section 1.2.1), or through extrinsic events related to habitat loss or natural enemies [49]. Metapopulation level extinction can also result from environmental stochasticity at the regional scale [17], provided this stochasticity is spatially autocorrelated, such that it is expected to promote synchronous dynamics among habitat patches [46].

1.3.1 Basic Metapopulation Models and Extinction

In the classic metapopulation model described by Richard Levins, the balance between patch colonization (c) and local extinction (e) determines patch occupancy dynamics. In this case, local habitat patches are either occupied or unoccupied, and both patch number and the spatial orientation of patches are undescribed. It is important to note that in a metapopulation, there are two levels of extinction; individual habitat patches may go extinct, or the entire metapopulation may go extinct. Dispersal among habitat patches can rescue patches from extinction or allow for the recolonization of extinct patches. This becomes more important when we consider dispersal dynamics, subpopulation synchrony, and environmental stochasticity.

The basic formulation of the Levins model is

$$\frac{dP}{dt} = cP(1-P) - eP, \tag{1.3.1}$$

where the balance between e and c determines long-term persistence of the metapopulation [67]. A necessary condition for metapopulation persistence in this model is

$$\frac{e}{c} < 1, \tag{1.3.2}$$

where, at equilibrium, the patch occupancy is given as

$$\hat{P} = 1 - \frac{e}{c} \tag{1.3.3}$$

In this model, the mean time to extinction of any given population is the inverse of the rate (i.e., $T_E = 1/e$), providing a link to the models at the population scale discussed above.

We can take the Levins model a step further to explicate the relationship between patch occupancy and overall mean time to extinction T_M at the metapopulation scale. Starting with the assumption that each of the H patches has its own average extinction time T_L (which should be the inverse of e), we have

$$T_M = T_L \exp\left(\left(\hat{P}H\right)^2 / \left(2H(1-\hat{P})\right)\right). \tag{1.3.4}$$

Consequently, using Eq. (1.3.3), we can also express T_M as

$$T_M = T_L \exp\left(\frac{H}{2}\left(cT_L + \frac{1}{cT_L} - 2\right)\right), \tag{1.3.5}$$

showing that metapopulation extinction time increases exponentially, not linearly, with the MTE of individual habitat patches [48].

The Levins model is mathematically equivalent to a logistic model, a well-developed model often used to examine single species population dynamics. The simplicity of the Levins model has resulted in a sizable body of literature surrounding and extending the model. For instance, in the original Levins model all patches are equidistant from one another, identical in quality, and can only be in one of two potential states (occupied or unoccupied), but each of these conditions is frequently adjusted in derivative stochastic patch occupancy models (SPOMs). Researchers have shown that despite the simplicity, Levins-type dynamics can emerge from more complicated stochastic metapopulation models [33], and extensions of the Levins model continue to provide insight into the influence of habitat patch size and topography (i.e., spatial orientation of habitat patches) on metapopulation persistence [42].

Island Biogeography and Metapopulation Capacity. A simple extension of the Levins model considers a set of spatially explicit patches of variable size, where a distance matrix D describes the distance between all patches in the metapopulation. The model borrows elements of Island Biogeography Theory [71], such that distance between patches (D_{ij}) and patch area (A_i) influence extinction and colonization processes, where the extinction constant (e) is modified for each patch based on area ($e_i = e/A_i$) and colonization becomes a property of distance (D_{ij}), patch area

(A_i), and dispersal rate (α),

$$c_i = e^{-\alpha D_{ij}} A_j p_j(t). \tag{1.3.6}$$

This suggests that the mean time to extinction of a habitat patch ($1/e_i$) is determined by the area of the patch. This makes the occupancy probability of each patch in the metapopulation, described in terms of matrix M,

$$M_{ij} = e^{-\alpha D_{ij}} A_i A_j, \tag{1.3.7}$$

and the leading eigenvalue of this matrix M describes the persistence of the metapopulation (*metapopulation capacity* λ_m [50]). The condition for metapopulation persistence is that the dominant eigenvalue of M must be greater than the ratio between extinction and colonization rates,

$$\lambda_M > e/c. \tag{1.3.8}$$

Since habitat patches vary in their size and connectedness to other patches, it is possible to determine the relative importance of each habitat patch to metapopulation persistence in this framework [47, 50], potentially informing conservation and management decisions [103]. While spatially explicit, this approach does assume that dispersal among habitat patches is determined by patch area and distance to other patches, ignoring population dynamics in each patch.

Incorporating Patch Dynamics. The above extension of the Levins model allows for patches to vary in size and connectedness. Another extension is to consider the abundances of habitat patches within the metapopulation, thus considering the dynamics of each patch and the effects of dispersal among local populations [90],

$$N_i(t+1) = R_i(t) N_i(t) e^{-N_i/K}. \tag{1.3.9}$$

This expression assumes that the growth rate of each habitat patch is R_i and that the carrying capacity is a constant K. If we assume that the population growth rates (r_i) are *iid* Gaussian random variables, this causes R_i values to be log-normally distributed and allows us to define persistence thresholds for the metapopulation based on the variance in the population growth rates r_i. The threshold for metapopulation persistence relies on exceeding a threshold value (σ_{th}) in terms of the variance among local patch population growth rates (r_i). This threshold is

$$\sigma_{th} > \sqrt{2|\mu_i|}, \tag{1.3.10}$$

where μ_r is the mean local population growth rate over time. This model can be extended to yield many interesting conclusions. For instance, if populations have influence on where their offspring go, population growth rates may be maximized by seeding offspring in less than suitable "sink" habitat if habitat quality fluctuates with time, and when the "source" habitat occasionally experiences catastrophes [55]. The complexity of metapopulation dynamics in the face of environmental stochasticity,

variable patch quality, dispersal, and competition has fueled some great theoretical work [12, 73]. An obvious next step is to scale from single species metapopulations to multi-species communities (i.e., metacommunities), which allows for the modeling of how species interactions, predator-prey dynamics, and community assembly relate to persistence [66].

1.4 The Species Scale

Extinction is defined at the scale of the species, but it is also at this level of taxonomic resolution that it is perhaps hardest to quantify—and, to summarize—due to considerable diversity of approaches and applications. We explore in this section two applied extensions of that body of theory, corresponding to two common quantitative frameworks for species-level extinctions. In the first, the complete loss of suitable habitat leads to an inevitable—if not immediate—extinction. Species can escape extinction through three primary channels: acclimation, adaptation, and migration. Species distribution models are often used to calculate extinction risk at the community scale in that framework (described in greater detail below), but they can only at best include the last of those three rescue processes. Evolutionary models, on the other hand, can link demography and genetics to the overall risk of extinction in a changing environment. We explore that application here in the context of both adaptation and phenotypic plasticity.

The second framework is based on the notion that population extinctions become species extinctions; and so the framework for population (and metapopulation) viability analysis described above acts as a sufficient method for estimating species extinction risk. In many cases, that may be a safe assumption, as near-extinction species are reduced down to a single persistent population or a handful in isolated refugia. But in real applications, persistence in small isolated refugia may be difficult to study, or even observe with any regularity; consequently, an entire body of literature has been developed to relate extinction risk to the sightings of rare species. That body of theory allows two applications: the posthumous assignment of extinction dates to extinct species, and sighting-based hypothesis testing for a species of unknown extinction status. We explore both applications briefly below.

1.4.1 Adaptation and Plasticity in a Changing Environment

Bounding uncertainty is the seminal challenge to extinction research, and in the real world, species' potential to acclimate and adapt to changing environments confers an unknown degree of robustness that has the potential to give species a chance at evading extinction. As discussed above, evolutionary rescue has been a particularly tantalizing—and controversial—idea in the context of disease research. But more broadly, evidence suggests that extinction risk is heavily complicated by species'

variable ability to track changing climates (and, more broadly, changing environments).

Most models that estimate the potential for evolutionary rescue approach the problem by explicitly modeling fitness curves and the speed of natural selection. In a foundational paper by Gomulkiewicz and Holt [44], an environmental change beginning at time 0 is followed by changes determined by fitness W such that

$$N_t = \bar{W}_{t-1} N_{t-1} = \prod_{i=1}^{t-1} W_i N_0. \tag{1.4.1}$$

If the population has a critical density N_c below which extinction is certain—essentially, a pseudo-extinction threshold in a PVA framework—extinction time is evolutionarily fixed without adaptation (i.e., $W_t = W_0$),

$$T_E = \frac{\ln N_c - \ln N_0}{\ln \bar{W}_0}. \tag{1.4.2}$$

To address evolutionary potential, Gomulkiewicz and Holt adapt Lande's equations, which describe the rate of natural selection on a single phenotypic trait [63]. In their notation, the trait z has an optimum phenotype normalized to zero, making d_t the distance of observed phenotypes from optimal phenotype at each time step, and d_0 the initial distance (i.e., the initial mean phenotype of the population). Any individual phenotype z is normally distributed around d_t in a distribution p that determines fitness,

$$p_t[z] \sim \mathcal{N}(d_t, {\sigma_z}^2) \tag{1.4.3}$$

The corresponding fitness function with width ω_z is expressed as

$$W(z) = W_{\max} e^{-z^2/(2\omega_z)}, \tag{1.4.4}$$

where $W_{\max}$ is the fitness at $z = 0$. The same expression can also be used to describe the overall tendency of the system,

$$\bar{W}_t = W_{\max} \sqrt{\omega_z/(\sigma_z^2 + \omega_z)}\, e^{-d_t^2/(2{\sigma_z}^2 + 2\omega_z)}. \tag{1.4.5}$$

The expression can be mildly simplified by defining $\hat{W}$ such that it is the growth rate of the optimum mean phenotype population,

$$\hat{W} = W_{\max} \sqrt{\omega_z/(\sigma_z^2 + \omega_z)}. \tag{1.4.6}$$

How does the actual distribution of phenotypes change over time? In real systems, evolution is seldom a direct progression towards the optimum, even under hard selection with ample genetic variation. If the trait z has a heritability h^2, they define an "evolutionary inertia,"

$$k = \frac{\omega_z + (1-h^2)\sigma_z{}^2}{\omega_z + \sigma_z{}^2}; 0 \leq k \leq 1 \tag{1.4.7}$$

$$d_t = k^t d_0 \tag{1.4.8}$$

which together produce a governing expression for the system,

$$t \ln \hat{W} - \frac{d_0{}^2}{2(\omega_z + \sigma_z{}^2)} \frac{1-k^{2t}}{1-k^2} = \ln \frac{N_c}{N_0}, \tag{1.4.9}$$

If this equation has no roots when solving for t, then this indicates the population will fall and rise without any real extinction risk. But when it does, the roots are estimates of the time until the population falls below the critical threshold (T_E) and the time until recovery could be evolutionarily possible (T_P in their notation, where N_t passes back above N_c). The interval between these two values is characterized by a small population that, due to demographic stochasticity, would require much more intensive conservation efforts (e.g., managed *ex situ* breeding) than normal to possibly survive that interval. The time to recovery (growth switches from negative to positive even though $N_t < N_c$) is

$$T_R = \frac{1}{\ln k^2} \left(\ln \ln \hat{W} - \ln \frac{d_0{}^2}{2(\omega_z + \sigma_z{}^2)} \right). \tag{1.4.10}$$

From this expression, Gomulkiewicz and Holt derive a useful finding: "t_R increases logarithmically with the degree of initial maladaptation ... but is independent of the initial population density."

The model developed by Gomulkiewicz and Holt sets useful theoretical bounds on the genetically-coded evolution of a trait. But in the real world, phenotypic plasticity represents some of the most difficult to quantify potential for species to escape extinction. In an extension of similar models developed by Chevin *et al.* [22], the trait z has a developmental trajectory with both a genetic component and the potential for phenotypic plasticity in response to an environmental gradient ε. Their model uses a "reaction norm" approach to plasticity (popularized by Schlichting, Pigliucci and others [95]), breaking down that phenotypic trait into an adaptive genetic component a and a plastic component b that responds to the environmental gradient. They express the distribution of the phenotype $p(z)$ at generation n in an environment changing at rate $\varepsilon = \eta t$ as

$$p(z) \sim \mathcal{N}(\bar{z}, \sigma_z{}^2), \tag{1.4.11}$$

$$\bar{z} = \bar{a} + b\eta\big(T(n-\tau)\big), \tag{1.4.12}$$

$$\sigma_z^2 = \sigma_a{}^2 + \sigma_e{}^2, \tag{1.4.13}$$

where T is the generation time, developmental plasticity takes effect at time τ during ontogeny, and the strength of plasticity b (the slope of a phenotypic reaction norm) does not evolve over time. Assuming there is an optimum phenotype $\theta = B\varepsilon$, they define a changing population size with a maximum growth rate $W_{\max}$, such that

$$W(z) = W_{\max} \exp\left(-\frac{(z-\theta)^2}{2\omega_z} - \frac{b^2}{2\omega_b}\right), \tag{1.4.14}$$

where both ω's represent the strength of stabilizing selection (the width of fitness curves, comparable to above). From there, they make the link to overall population dynamics, where the intrinsic growth rate r of the population can be scaled with generation time and related to selection on z,

$$r = \frac{\ln(\bar{W})}{T} = \frac{\ln(W_{\max})}{T} - \frac{\ln(1+\sigma_z^2/\omega_z) + b^2/\omega_b}{2T} - \frac{(\bar{z}-\theta)^2}{2T(\omega_z+\sigma_z^2)}, \tag{1.4.15}$$

where the first two terms become the maximum possible growth rate $r_{\max}$ if z reaches the optimum θ.

From the expression for population dynamics, Chevin *et al.* derive a formula for the critical rate of environmental change, above which plasticity and adaptation cannot prevent extinction,

$$\eta_c = \sqrt{\frac{2r_{\max}\gamma}{T}}\,\frac{h^2\sigma_z^2}{|B-b|}. \tag{1.4.16}$$

From this expression, it is easy to determine the long-term tendency of the population to extinction or survival as a function only of the degree of plasticity and the associated strength of costs (ω_b). The greater the extent of plasticity, the more the costs of plasticity separate out population trajectories; but when plasticity has a weak slope, the extinction isoclines converge towards the same threshold. While this conceptualization of adaptation to environmental change as a single-trait system with readily measured costs of adaptive plasticity is obviously an idealization, it also clearly illustrates a number of important points. While adaptive genetic variation has a clear direct relationship to evolutionary rescue, plasticity also plays an important role; and quantifying plasticity without quantifying its costs can provide a misleading perspective on the feasibility of adaptation and acclimation.

Is Evolutionary Rescue Real? Evolutionary rescue is not a "silver bullet," and the application of evolutionary theory to real populations and metapopulations is far from straightforward. For one thing, evolutionary rescue requires a sufficiently large population that a species is buffered against extinction long enough for higher-fitness phenotypes to become predominant [51]. Additional complications include, but are not limited to

- **Initial environmental conditions.** Bell and Gonzalez showed that populations that begin at intermediate stress levels may react the slowest to environmental "deterioration," producing a U-shaped curve in adaptive rescue [10]. They explain this as a product of two competing processes driving evolutionary rescue: as baseline stress increases, overall mutation rates decline, but the proportion of beneficial mutations (or, perhaps more accurately, the associated fitness differential) increases. Populations beginning in "mildly stressful conditions" may simply be at the low point of both processes. Bell and Gonzalez similarly show

that populations with a history of minor environmental deterioration have a much greater probability of evolutionary rescue in a fast-changing environment.

- **The velocity of environmental change.** As Chevin *et al.*'s model highlights, environmental changes that are too rapid almost invariably drive species to extinction, when selection simply cannot operate fast enough to keep pace; this finding is readily confirmed in environmental settings. Rapid environmental changes can also functionally reduce mutation rates at a population scale. A study of *E. coli* by Lindsey *et al.* showed that "The evolutionary trajectory of a population evolving under conditions of strong selection and weak mutation can be envisioned as a series of steps between genotypes differing by a single mutation," and some "priming mutations" may be necessary to arrive at further genotypic combinations with substantially higher fitness [69]. Consequently, if environmental changes are too rapid, higher fitness genotypes may be "evolutionary inaccessible."
- **Dispersal rates and metapopulation connectivity.** Simulated metapopulation models by Schiffers *et al.* showed that higher dispersal rates can severely limit the propensity of populations to experience local adaptation, especially in a heterogeneous environment (a phenomenon they refer to as "genetic swamping"), and thereby potentially limit evolutionary rescue [94]. However, for an entire species to persist, intermediate (local) dispersal may be necessary to allow adaptive mutations to spread, a finding shown experimentally by Bell and Gonzalez.
- **Linkage disequilibrium.** Schiffers *et al.*'s study, which simulated genomes in an "allelic simulation model," produced an unusual result suggesting that linkage between adaptive loci may not actually increase the rate of adaptation. The interaction this could have with the "priming mutation" process is complex and poorly explored in a theoretical context.

A final important consideration should be made with regard to what Schiffers *et al.* distinguish as *complete* vs. *partial evolutionary rescue.* In their models, they find that when adaptive traits originated but spread poorly (as a combination of linkage disequilibrium, habitat heterogeneity, and dispersal limitations), it substantially reduced population sizes and ultimately produced an "effective reduction in the suitable habitat niche." This type of partial evolutionary rescue could be most common in real-world scenarios, where adaptation in larger populations experiencing the slowest rates of environmental change may allow persistence but not maintain a species throughout its entire range, and may still be followed by a substantial reduction in overall habitat occupancy.

If current research on global climate change is any indication, this type of partial evolutionary rescue may ultimately be a poor buffer against extinction. Climate change may set the events of an extinction in motion, but research suggests that habitat loss from climate change is rarely the direct and solitary causal mechanism of an extinction [14]. Instead, climate change may reduce a population to small enough levels at which other mechanisms drive extinction. Small populations are especially susceptible to stochastic crashes in population size, and may also be especially susceptible to stochastic collapse due to other factors within-species (Allee effects in breeding, inbreeding) or from interactions with other species (competition, invasion, disease). Ultimately, the synergy between these drivers may produce

a greater overall extinction risk that many modeling approaches might not directly quantify, but that could be most likely to drive species to extinction and ecosystems into novel assemblages [8].

1.4.2 After Extinction: Lazarus Species, Romeo Errors, and the Rarest Birds in the World

The job of conservation biologists and extinction researchers is far from over after the extinction of a species. The *auto-ecology* of an extinct species (its basic biology, ecology, natural history, distribution and other species-level characteristics) often becomes a permanent unknown, assumed to be lost to the annals of history. But as statistical tools for ecological reconstruction become more sophisticated, researchers have the opportunity to explore basic questions about extinction in retrospect. In particular, the same body of theory that governs the timing of extinction in a declining population can be applied in a retrospective sense as well, to estimate the likely extinction date of a species. (Or, more formally, the estimation of the MTE from a given point can be used to pinpoint T_E , even with the same data, after extinction has already occurred.) These methods have been used both for ancient species like the megalodon [82] and for more recent extinctions like that of the dodo [88]. But perhaps most interestingly, the theory can be applied when the uncertainty bounds on T_E contain the present date, meaning that the extinction of a species is not taken as a certain part of history. Even ancient "Lazarus species" can be rediscovered, like the coelacanth, believed to have gone extinct 66 million years ago but rediscovered in the last century. How can we confidently say the coelacanth continues to exist, but the megalodon is likely to never be rediscovered?

Basic Statistical Methods for the Sighting Record. Once a species is suspected to be extinct, at what point do we stop looking for them? With limited resources for conservation, trying to find and conserve a species that is no longer around wastes resources better used elsewhere/ But making a type I error and assuming a species is falsely extinct (and abandoning conservation efforts) can lead to a "Romeo error," whereby giving up on the species can lead to actual extinction [25]. Since 1889, 351 species thought to be extinct have been "rediscovered" [93], highlighting just how big of a problem this may be. In order to answer these questions, determining the probability that a species is still extant, despite a lack of recent sightings, is an important tool in making evidence-based decisions conservation managers must make about allocating resources.

Consider the plight of the ivory-billed woodpecker *Campephilus principalis*), a charismatic and iconic partFmass of the North American fauna. The ivory-billed woodpecker's decline was gradual, and unlike its gregarious and easily-spotted compatriots (such as the passenger pigeon, *Ectopistes migratorius*, or the Carolina parakeet, *Conuropsis carolinensis*, both extinct in a similar time period), sightings of the woodpecker were already rare previous to its decline. So while the bird's last "cred-

ible" sighting was in 1944, the precise date of its extinction remains controversial, and some believe the bird still exists based on unverified observations as recent as 2004 (with audiovisual evidence reviewed in a highly controversial 2005 paper in *Science* [37]). These controversial observations led to one of the most costly surveys in history, yet yielded no new evidence. In some circles, the search continues; in 2016, two ornithologists—Martjan Lammertink and Tim Gallagher—traveled through Cuba searching for remaining populations of the elusive woodpecker. Was Lammertink and Gallagher's search justified from a statistical standpoint?

But how do we determine the likelihood that a species is extinct? How long does it have to be since the last time an individual was seen before we can say, with some certainty, that the species is, in fact, gone? The most obvious step is to assemble all available evidence of when the species was around. The first place to look is in the specimen record, since this is the "gold standard" of evidence. However, other data can be brought to bear, including observations, photos, and audio recordings. All these forms of evidence are collectively referred to as *sightings*. In 1993, Andrew Solow developed an approach to resolve the extinction date of a species based on sighting records [98]. In Solow's notation, sightings in a period of surveillance between time 0 and time T occur at the dates $(t_1, t_2, ..., t_n)$ as a random process governed by a fixed sighting rate m that becomes 0 at T_E, the true date of extinction. The probability of the data conditional on a current time T and an extinction date T_E, is

$$P(T_n \leq t_n | T_E \geq T) = (t_n/T)^n. \tag{1.4.17}$$

In that light, Solow says, hypothesis testing is easy: against the null hypothesis that extinction has yet to happen (i.e., $T_E > T$), we can test the alternate hypothesis that the species is extinct ($T_E < T$). For a given last sighting at T_N, we can provide a p-value for the test with desired significance level α equivalent to

$$P(T_N \leq \alpha^{1/n} T | T_E < T) = \alpha (T/T_E)^n \tag{1.4.18}$$

for values of $\alpha^{1/n} T < T_E < T$; for values of T_E lower than or equal to that critical value $\alpha^{1/n} T$, the value of P is equal to 1 and the null hypothesis is rejected with full certainty. Solow explains, by way of example, that with 10 sightings and 95% confidence, the critical value of T_E/T is 0.74, and so the null hypothesis is sure to be rejected (extinction is confidently confirmed) if the true extinction date occurs within the first 74% of the $(0, T)$ window.

Solow similarly constructs a Bayesian approach, where the likelihood of the sighting data given H_0 is

$$\int_0^\infty m^n e^{-mT} dP(m), \tag{1.4.19}$$

and given H_A is

$$\int_0^\infty m^n e^{-mT_E} dP(m). \tag{1.4.20}$$

From these and other assumptions, he derives the Bayes factor for the hypothesis test (a metric that does not depend on prior assumptions, which expresses the

posterior: prior odds of H_0),

$$B(t) = (n-1)/\left((T/t_n)^{n-1} - 1\right). \tag{1.4.21}$$

Finally, from the original formulation of Solow's approach, we can also derive a maximum likelihood estimate of the extinction date [99],

$$\hat{T_E} = \frac{n+1}{n} t_n, \tag{1.4.22}$$

and, in addition, a $1-\alpha$ upper confidence interval bound,

$$T_E^u = t_n/\alpha^{1/n}. \tag{1.4.23}$$

Does this approach make sense? If an extinction happens abruptly on the scale of sightings data (say, an epidemic wipes a species out within a year), then sighting rates might remain relatively constant throughout the sighting record. Similarly, applying this method to paleontological records may make sense, as prior information about variation in specimen preservation might be limited (and so a constant rate parameter is the best possible prior). But there are also a number of situations where the constant sighting rate m simply does not suffice. Lessons from population ecology remind us that extinction is, at its most fundamental scale, a process of declining abundance. If sightings are dependent on abundance (which they generally are), replacing m with a non-constant function has the potential to sharply refine the process of extinction date estimation.

Similarly, not all sightings are created equally. If you are holding a dead body of an individual of the species in question, that is good evidence the species was present the year the specimen was collected. Conversely, if some person claims they saw an extremely rare species with no corroborating evidence, that person may have misidentified the individual, or in some cases even lied, meaning that this sighting could be be invalid. Roberts *et al.* found that these approaches are sensitive to the data used and can, unsurprisingly, lead to very different estimates of extinction dates [87]. They partitioned sighting data into three categories: 1) physical evidence, 2) independent expert opinion, and 3) controversial sightings in order of certainty. They found that adding independently-verified observations to the analysis can sometimes lead to earlier predicted extinction times, since the "gaps" within the sighting record are closed up, whereas, by nature, later controversial sightings, if treated as legitimate (i.e., on par with physical evidence), can greatly push the estimates of extinction to later years. To account for this uncertainty, a few approaches have been proposed recently. These approaches largely expand on Solow's 1993 Bayesian equation above, modified to consider multiple levels of uncertainty in the data [65, 100, 104]. For an overview of the assumptions and relative strengths of these approaches, see Boakes *et al.* [11].

Finally, some nonparametric approaches to extinction date estimation focus on the last few sightings of a species, rather than the entire record of their observations. Solow [99] notes two such methods in a review that covers these methods of

estimations in much greater depth. The first, originally suggested by Robson and Whitlock [89], just uses the last two sightings,

$$T_E = t_n + (t_n - t_{n-1}), \tag{1.4.24}$$

with a fairly clear reasoning: if a large gap exists between the last two sightings, conservation biologists should wait at least that long before pronouncing a species certain to be extinct.

In contrast, the second and far more complex method designed by Solow (and implemented by Roberts and Solow in their 2003 study of the dodo [88]) accounts for the fact that the last few sightings of the species should, in most circumstances, follow a Weibull distribution. The method, *optimal linear estimation* (OLE), estimates T_E through linear algebra,

$$T_E = \sum_{i=1}^{k} w_i t_{n-i+1}, \text{ where } w = (e'\Lambda^{-1}e)^{-1}\Lambda^{-1}e. \tag{1.4.25}$$

Here, e is a column vector consisting of k 1's and Λ is a $k \times k$ matrix with elements

$$\Lambda_{ij} = \frac{\Gamma(2\hat{v}+i)\Gamma(\hat{v}+j)}{\Gamma(\hat{v}+i)\Gamma(j)}, \text{ where } \hat{v} = \frac{1}{k-1}\sum_{i=1}^{k-2} \ln \frac{t_n - t_{n-k+1}}{t_n - t_{i+1}}. \tag{1.4.26}$$

While the OLE method is obviously much less transparent, it has been recorded as one of the most successful methods available for predicting extinction [24], and has the added bonus of being adjustable through sensitivity analysis to examine how different extent of sighting data changes the overall estimate.

Case Study: Spix's Macaw. Perhaps the most fruitful body of research concerning extinction date estimation has been within ornithology, where data on the last sightings of rare species is often more available than for other groups, due to tremendous global interest in bird sightings and observation by non-scientists. The most popular methods for sighting date research have often been developed in association with data on notable extinct birds, including the dodo, the passenger pigeon, and the ivory-billed woodpecker. In fact, one of the most expansive reviews of sighting date estimators, conducted by Elphick, estimated the extinction date of 38 extinct or near-extinct birds from North America (including Hawaii, a hotspot of bird extinction) [35]. But for rarer birds around the world, basic data on their extinction may be somewhat more lacking.

One such bird, the Spix's macaw (*Cyanopsitta spixii*) has been called "the world's rarest bird" [57] and has been the subject of two popular animated movies (Rio and Rio 2). Currently, Spix's macaw is considered critically endangered (possibly extinct in the wild) by the IUCN (2016), with a small number of captive individuals ($\sim$130) found around the world. Not seen in the wild since 2000, a video of a Spix's macaw in Brazil made headlines in 2016. The video was subsequently examined by ornithologists, and the consensus that the bird was, in fact, a Spix's macaw, though many still believe the bird was likely an escaped captive bird.

Sightings of the Spix's macaw are sporadic, and after the first known specimen being shot in 1819 by Johann Baptist Ritter von Spix (though he believed the bird to be a Hyacinth Macaw), it was not recorded again until a wild-caught individual was procured by the Zoological Society of London in 1878. Collecting sighting records of the Spix's macaw relies mostly on data from trappers/poachers and inferring data from captive individuals. Given the illicit nature of wildlife poaching, better data may exist in the husbandry records of the wild-caught individuals currently in captivity, but those data are not freely available. Verifiable observations are few and far between, as this species was not subject to any intensive study or searches until the mid-1980s, when only a handful of individuals were found and, of those remaining, most were caught by poachers.

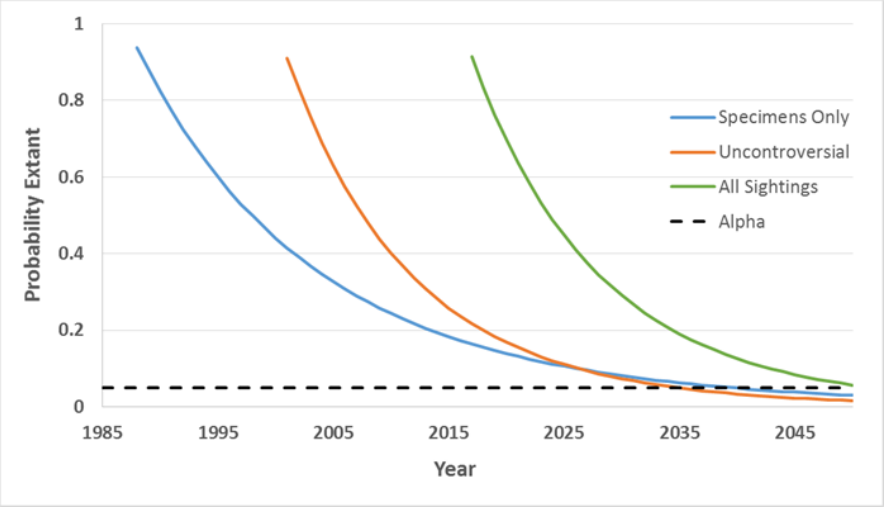

Fig. 1.4.1: Estimates of likely extinction date of the Spix's macaw based on extinction estimating equations in Solow (1993). The lines represent the estimated probability the species is extant each year; the blue line is the results using physical evidence only (specimens / wild-caught individuals), the orange line for uncontroversial sightings *and* physical evidence, and the green line is the results for all sightings, including controversial. The dotted line is a significance level of 0.05. Once the probability drops below this level, the species is considered likely extinct.

For this case study, we collected sighting and specimen data from GBIF (Global Biodiversity Information Facility; `www.gbif.org`) and Juniper's authoritative book on Spix's macaw. We found physical evidence (specimens and wild-caught captive birds) for sightings in the years 1819, 1878, 1884, 1901, 1928, 1954, 1977, 1984, 1985, 1986, and 1987. Due to their rarity and the demand for them, we assumed individuals were caught in the wild the same year they were procured by the receiving institution or zoo. We considered all observations of the Spix's macaw

reported in Juniper's book as verified, as there aren't many and these few have been rigorously scrutinized: 1903, 1927, 1974, 1989, 1990, and 2000. Our only controversial sighting is the recent video taken in 2016. Taking the approach by Roberts *et al.*, we partitioned the data into three datasets: 1) physical data only, 2) physical plus verifiable observation data, and 3) all data (including the controversial sighting). By eliminating the controversial sighting (in analyses 1 and 2), we inherently test a methodological question: would extinction date estimators have pronounced the apparently-extant species dead?

Our analysis was conducted using the beta version of the `R` package `sExtinct`, which allows a handful of different extinction analyses to be implemented [23]. (We encourage prospective users to test the demos available with the package.) Our analysis uses two of the most common methods. First, we used the original Solow maximum likelihood approach, plotting the probability of persistence in Figure 1.4.1. The maximum likelihood estimates are given in that method as

- Specimens only: $T_E = 2040$,
- Uncontroversial sightings: $T_E = 2035$,
- All sightings: $T_E = 2052$.

The method suggests, even with the most limited dataset, that the species still appears to exist. In contrast, the OLE method tells a different story:

- Specimens only: $T_E = 1988$ (95% CI: 1987 - 2006),
- Uncontroversial sightings: $T_E = 2002$ (95% CI: 2000 - 2018),
- All sightings: $T_E = 2021$ (95% CI: 2016 - 2045).

All things considered, both analyses suggest a chance the 2016 sighting may have been legitimate, and there is a possibility that a wild population of Spix's macaws may be out there, yet undiscovered in the Amazon rainforest. But, the OLE method—for all its documented strength as an approach—would likely have been far hastier to dismiss the species as extinct before its 2016 "rediscovery." Furthermore, it currently only predicts another five years of persistence for the species, and with some researchers hoping to use extinction date estimators as a method of Red Listing, the Spix's macaw clearly remains a severely threatened species.

Hope Springs Eternal: the Ivory-Billed Woodpecker and the Hunt for More Lazarus Species. To briefly reconsider Lammertink and Gallagher's continuing search for the ivory-billed woodpecker: regardless of how the sighting record for the ivory-billed woodpecker is analyzed, all indications point to an extremely low likelihood that the species is extant [35, 45, 100]. In the work of Elphick *et al.*, estimates based on physical evidence suggested a T_E of 1941 (upper 95% CI: 1945) and including expert opinion sightings only moves T_E towards 1945 (upper 95% CI: 1948). With other models hardly disagreeing on the scale of a full century, the hard evidence available to modelers casts serious doubts on the validity of the species' "rediscovery" in 2004 [96], or further, justify the subsequent, costly search to find more conclusive evidence of the ivory-billed woodpecker's existence. Some argue the search continues as long as hope does, but statistics has a somewhat different answer in this case. And with other species like the Spix's macaw still potentially

within the bounds of rescue, the resources of conservation organizations might be better devoted to saving those species than to chasing the ghosts of woodpeckers past.

Once it is determined that there is an acceptable level of probability that a species is extant, one possible way to further leverage the data collected would be use the data to build species distribution models (SDMs) to aid in the search and rescue effort. In basic terms, SDMs use information about the conditions where a species has occurred (and where it has not occurred) to determine the realized niche of the species. This niche can be projected onto geographic space to help identify areas areas that appear highly suitable for the species but perhaps have not been searched yet. This approach has been successful in identifying new populations of threatened species (e.g., see [75]), with the author identifying new populations of four of the eight rare plant species in the study. While SDMs are commonly used in a variety of different ecological and conservation applications, there is a deep literature on comparisons of SDM methods (see Qiao *et al.* [84] for an overview), so much caution must be used in selecting which methods are best for the available occurrence and environmental data. This approach—of determining the probability a species is still extant and using SDMs to identify the areas they are most likely to be—may provide a way forward for conservation agencies for making cost-effective decisions of which species to pursue and where to look for them.

1.5 The Community Scale and Beyond

Suppose that, in a twisted experiment motivated by an ecology-related childhood trauma, a mad scientist was developing a scheme to reduce global biodiversity to one half of the Earth's total species. Hunting, fishing and poaching could achieve that goal slowly but would be particularly inefficient for eradicating insects; and while a generalist disease might help eradicate a handful of mammals or a sizable fraction of amphibians, the majority of species would still remain. But perhaps realizing that habitat loss might be the most efficient tool to destruction, the mad scientist might cut the Gordian knot by simply bisecting the Earth and destroying one half. Would his plan come to fruition?

Our mad scientist's plan is riddled with flaws. If one half of the species were endemic to each half of the Earth with no overlap, his plan would succeed. But a handful of species in any clade of life are globally cosmopolitan; and no matter how his plan was executed, the handful of species occurring on both halves of the Earth would leave him with far, far more than half the species he started with.

With renewed vigor, the mad scientist sets out on a newly ambitious project: what percentage scorched earth would be required to achieve his goal? He begins by counting every species on his sidewalk block, then in his neighborhood, and up to bigger scales. With enough grant funding and undergraduate assistants, he has eventually covered a measly 6.25% of the Earth when he realizes he has counted half of Earth's species. To enact his master plan, he's tasked with destroying the re-

maining 93.75%. Going by land area alone (his grudges, we suppose, do not extend to the ocean), he only needs preserve 3.6 million square miles of land—roughly (conveniently?) the land area of the United States.

The process our nationalist, isolationist villain has enacted is the empirical construction of the species–area relationship (SAR), one of the oldest and most powerful scaling laws in macro-ecology. Because the synthesis of different factors at global scales is challenging, and habitat loss is one of the easiest extinction drivers to measure, the SAR gives us a powerful tool for approximating extinction rates—at the price of not knowing specifically which species will go extinct.

1.5.1 The Species-Area Relationship

The biogeographer Olof Arrhenius began the process of formalizing the SAR in a classic 1921 paper entitled "Species and Area" in the *Journal of Ecology* [6]. Arrhenius observed that, by expanding the area of focus, the number of species continues to increase at a diminishing rate (but, never reaching an asymptote [107]). The canonical formula for the SAR has come to be called the Arrhenius SAR, and is formulated as

$$S = cA^z,$$

where c is a constant fit to the data and z is a slope, conventionally taken as 0.25. The application of this formula to extinction rate estimation is relatively obvious; by changing the amount of area, we can change the number of species,

$$S' = c(A')^z,$$

and calculate the number of extinctions

$$E(A') = S - S'.$$

In our mad scientist's failed scheme, reducing the area of the Earth by half would leave us with far more than half the species,

$$\frac{S'}{S} = \left(\frac{0.5A}{A}\right)^{0.25} = (0.5)^{0.25} = 0.84.$$

In a 2004 *Nature* paper that has become the most cited study on extinction since the millennium, a group of researchers led by Chris Thomas refined the global extinction rate estimate by analyzing species' habitat losses from climate change and applying the SAR. Their extinction-area relationship took three forms applied to n species, with a given A_i area per species before change, and A_i' subsequent to habitat loss,

$$E_1 = 1 - \left(\frac{\sum\limits_{i \in (1,n)} A_i'}{\sum\limits_{i \in (1,n)} A_i} \right)^{0.25},$$

$$E_2 = 1 - \left(\frac{1}{n} \sum_{i \in (1,n)} \frac{A_i'}{A_i} \right)^{0.25},$$

$$E_3 = \frac{1}{n} \sum_{i \in (1,n)} \left(1 - \left(\frac{A_i'}{A_i} \right)^{0.25} \right).$$

Using those three methods in combination with species distribution models, the authors estimated that 15-37% of species on Earth might face climate-driven extinction by 2050. ThIs result is by far one of the most important ones produced in any study of extinction and has supported a number of the most expansive conservation programs worldwide.

1.5.2 Everything You Know About the Species-Area Relationship is Wrong

Like many "laws" of ecology, the conventional SAR has problems and pitfalls, and with the tremendous array of approaches developed to study it, it has even been called ecology's "most protean pattern" [70]. Subsequent to the publication of Thomas *et al.*'s study, one of the most seminal debates in extinction research has centered around its conclusion that climate change is likely to act as the most consequential driver of the sixth mass extinction. Different approaches to the species–area relationship and comparable or derivative macro-ecological methods have sprung up in the wake of Thomas's work. Here, we review a few of the different approaches that can be used to predict extinction rates at the community level.

***z*: A Dynamic Scaling Property.** The most immediate problem with applying the species–area relationship is that the slope z, normally set to 0.25, is neither universal nor scale-independent. In part, this is because of two different constructions of the SAR. The slope of 0.25 derives from the experimental work of Macarthur and Wilson on island ecosystems, which applied the SAR to the richness of species on islands of different sizes. For islands (and for application of the island SAR to extinction), a slope of 0.25 is justified under a set of three (relatively common) circumstances delineated by Harte and Kitzes: "(i) total abundance in the new area A is proportional to area, (ii) individuals found in A are chosen by a random draw from all individuals in A_0, and (iii) the number of individuals of each species in A_0 follows a canonical lognormal abundance distribution" [52].

However, the continental "nested" SAR (constructed from nested areas on a continental scale) does not always follow the same property. This is in part because the conventionally used SAR assumes self-similarity (or, in more tangible terms, pick-

ing two patches of different area always yields a roughly-the-same-slope difference in species). As it turns out, self-similarity works within some sites but not others, and within the Western Ghats mountains of India alone, scaling up from vegetation sampling plots to broader scales brings z down from values closer to 0.5 to values approaching 0 [53]. Selecting an appropriate slope based on scale is an important part of appropriate use of the SAR to predict extinction rates, and as analyses approach the continental scale, the appropriateness of the SAR method decreases as z approaches zero.

Alternate Approach Based on the Endemics Area Relationship. In the Thomas *et al.* study, the application of the species area relationship followed three methods, and while some explicitly predicted extinction risk at the scale of a single species, all rely on the prediction of reduced species richness based on habitat loss. In place of this indirect calculation of decreased richness, a more direct approach uses what is called the *endemics–area relationship* (EAR), which calculates the number of endemic species restricted to a given area (all of which should be committed to extinction when the area is destroyed). As pointed out by He and Hubbell, the SAR and the EAR are not mirror curves except in a single special case when species are completely randomly distributed in space; else, the "forwards" and "backwards" methods of extinction calculation are not, they argue, comparable [54].

Prediction of extinction based on the EAR may be more appropriate for measuring the immediate effects of habitat loss, and is likely to better account for the "geometry of habitat clearing" [59]. Storch *et al.* [101] developed an approach to the SAR and the EAR that scales the area by the mean geographic range size in the focal clade/area and scales richness by the average number of species in that mean geographic range. When plotted, the SAR curves upwards while the EAR is roughly linear with a slope of 1 across most scales. Starting from basic knowledge about the average geographic range size of a given species, this result indicates that extinction from habitat loss can be predicted based on the EAR across scales fairly accurately.

Alternate Approach Based on Maximum Entropy. Two "unifying" theories have dominated discussions about macro-ecology. The first is the unified neutral theory (UNT) of biogeography and ecology (proposed by Stephen Hubbell), which is beyond the scope of this chapter; the second is the maximum entropy theory of ecology (METE) proposed by John Harte. The METE deserves special mention here, due to a particular focus in the METE literature on improving the applicability of the SAR to extinction rate prediction. What differentiates both the UNT and the METE from more general conceptions of the SAR is the explicit treatment of species abundance as a component of community assembly. The theory of the METE is far too complex to encapsulate in this chapter (and an entire book by Harte exists for that purpose), but a few useful derivations are worth mentioning. One is the derivation by Kitzes and Harte of an extinction probability that is applicable at the species scale [52] based on proportional area loss (A_0/A, shortened to β) and corresponding reduction in abundance (n from n_0) with a general probability distribution

$$P(n|n_0, A_0, A) = ce^{-\lambda n}, \tag{1.5.1}$$

for which they provide rough approximations,

$$c \approx \frac{1}{(An_0/A_0)+1}, \quad \lambda \approx \ln\left(1+\frac{A_0}{An_0}\right). \tag{1.5.2}$$

Drawing on similar concepts from the pseudo-extinction thresholds we discuss above in Section 1.4.1, they suggest that the probability that a remainder $r_c = n/n_0$ is left after habitat loss is

$$\text{Prob}\left[\frac{n}{n_0} > r_c\right] = \int_{r_c n_0}^{n_0} ce^{-\lambda n}\, dn = \frac{[n_0\beta/(1+n_0\beta)]^{r_c n_0} - [n_0\beta/(1+n_0\beta)]^{n_0}}{(1+n_0\beta)\ln(1+1/n_0\beta)}. \tag{1.5.3}$$

Given a starting population and a critical population size, analogous results can be derived for the Thomas *et al.* calculations; higher level predictions can be made based on the distribution of abundances and critical abundances within the community.

In a subsequent publication [60], this *extinction-area relationship* is extended even further to extrapolate a MaxEnt-based probability that a given number of species will remain after habitat loss. It assumes a log-series distribution ϕ of abundance for species with a mean μ_ϕ, with a single shape parameter p,

$$\phi(n_0) = \frac{-p^{n_0}}{\ln(1-p)n_0}, \quad \mu_\phi = \frac{-p}{(1-p)\ln(1-p)}. \tag{1.5.4}$$

They similarly propose an upper-truncated geometric species specific abundance distribution, which provides the probability that n individuals remain in a fractionally reduced area a (β in their other notation) based on a shape parameter q,

$$\Pi(n|a,n_0) = \frac{(1-q)q^n}{1-q^{n_0+1}}, \tag{1.5.5}$$

where q is solved implicitly based on a and n_0 from the equation

$$an_0 = \frac{q}{1-q} - \frac{(n_0+1)q^{n_0+1}}{1-q^{n_0+1}}. \tag{1.5.6}$$

The probability that a species is found in area A after habitat loss follows a distribution g which takes the form

$$g(a,n_c) = \sum_{n_0=1}^{\infty} (1-\Pi(n\leq n_c|a,n_0))\phi(n_0), \tag{1.5.7}$$

which scales up to a community-level richness after area loss,

$$p(S|S_0,g) = \binom{S_0}{S} g^S (1-g)^{S_0-S}, \tag{1.5.8}$$

where

$$g(a,n_c,\mu_\phi) = \sum_{n_0=1}^{\infty}\left(1-\frac{q^{n_c+1}-1}{q^{n_0+1}-1}\frac{-p^{n_0}}{n_0\ln(1-p)}\right) \tag{1.5.9}$$

or, if the pseudo-extinction threshold is set to zero (i.e., no species has 0% survival odds until all individuals are dead) and area loss is severe, this expression can be reduced to eliminate the q term,

$$g(a,n_c,\mu_\phi) = -\frac{a}{\ln(1-p)}\sum_{n_0=1}^{\infty}\frac{p^{n_0}}{an_0+1}. \tag{1.5.10}$$

This METE approach thus provides a *probabilistic species–area relationship* (PSAR) that can be used to provide not only an expected extinction rate under habitat loss but also a range of confidence. This becomes an especially important tool in a small community of only a few dozen species or fewer (or in communities with pervasive low abundance across species), where deviations from SAR-based predictions may be greater due to stochastic processes.

How does the PSAR scale up against the Thomas-SAR? It has a clear advantage in the prediction of individual species extinction risk (but correspondingly requires more data on abundance/demography that may be absent for many poorly known taxa). Kitzes and Harte provide two illustrations. First, assuming the normal slope of 0.25, the PSAR predicts a 44% chance of extinction for a species that loses 90% of its habitat. Second, if we assume a pseudo-extinction threshold of 50 individuals, the Thomas-SAR under-predicts the extinction risk if n_0 is less than 1,000 but over-predicts otherwise.

Tying Up Loose Threads, Thinking Across Scales. The various different approaches to predicting extinction at the broadest scales have driven substantial controversy among different interpretations of macro-ecological theory. But one of the most important problems is that estimates of extinction from these methods are still poorly connected, by and large, to the rest of the extinction literature—and to the other types of models we discuss above. One of the most innovative and unusual approaches in the literature was presented by Rybicki and Hanski [91], who simulated a stochastic patch occupancy model (similar to those presented in Section 1.3.1) with spatially heterogeneous environmental conditions across patches. While their model incorporates the standard mainstays of an SPOM (colonization, extinction, a dispersal kernel), it also incorporates a phenotype and niche breadth that produce a Gaussian fitness function (like many of the models discussed in Section 1.4.1).

Tying together a number of the important ideas discussed above, the work of Rybicki and Hanksii made several advances into new territory. For one, they make a semantic distinction between the EAR (which they define as the $S = cA^z$ relationship applied to the area lost a) and the "remaining species–area relationship" (RAR),

$$S - S_{\text{loss}} \;=\; c(A_{\text{new}}/A)^z. \tag{1.5.11}$$

The EAR and RAR, as two methods of calculating extinction risk, are not interchangeable or symmetric counterparts. Rybicki and Hanskii highlight a discrepancy

between Storch *et al.*'s suggested EAR slope of roughly 1, and He and Hubbell's values which were a tenth smaller [54], which they suggest can be resolved by the fact that Storch fit the EAR while He and Hubbell were calculating the RAR. Their simulations agree with the results of He and Hubbell that the slope of the RAR may be half or less that of the SAR.

Their empirical approach to simulation leads to a valuable conclusion that stands in opposition to previous work. While Kinzig and Harte [59] and He and Hubbell [54] both strongly suggest that the SAR over-estimates extinction risk, the results of Rybicki and Hanskii's simulations suggest that in the short term, the RAR under-estimates extinction while the continental SAR ($z \approx 0.1$) is adequate. Their result ties the population scale to the community scale, as they attribute it to species' populations *outside* destroyed or fragmented habitat falling below critical thresholds and facing extinction despite the lack of total endemic extirpation. In the long term, they suggest, the island SAR ($z = 0.25$) may be the best predictor of total losses. Finally, they explore the difference between leaving a single patch of habitat and fragmenting habitat and conclude all models underestimate extinction risk in scenarios of extreme fragmentation. To address that problem, they propose a modified species area relationship

$$S = cA^z e^{-b/\lambda_M}, \tag{1.5.12}$$

where λ_M is the metapopulation capacity (see Section 1.3.1) and b is another scaling parameter like c and z. If n is the number of habitat fragments, they suggest, the metapopulation capacity scales linearly with A^3/n^2, meaning that the *fragmented landscape species area relationship* (FL-SAR) can be expressed as

$$S_{\text{new}}/S = (A_{\text{new}}/A)^2 e^{-bn^2/A^3}. \tag{1.5.13}$$

While the data to fit such an expression might be challenging to collect (and so the FL-SAR may not be an immediately useful conservation planning tool), the FL-SAR provides an important and much needed link between the population processes we discuss above and our broader understanding of the rate of extinction at landscape and community scales.

1.6 Last Chance to See

What don't we know about extinction yet?

As predictive tools gain precision, our estimates of the extinction rates of well-known groups like mammals and birds also become more precise. But the majority of the world's species are not yet known; most animal diversity is harbored by insects or parasites (especially nematodes), and the vast majority of species in those groups are undiscovered or undescribed. Their extinction rates are just as poorly quantified as their diversity, average range size or abundance distribution, or the hotspots of their biodiversity. But some basic estimates suggest that 7% of the planet's invertebrates may have already gone extinct—at which rate evidence would

suggest that 98% of extinctions on Earth are currently going undetected [86]. It is also especially difficult to compare these extinction rates to historical baselines, because the fossil record for most invertebrates and other taxa are incomplete or nearly absent.

An especially poignant problem is the detection and estimation of co-extinction rates—the secondary extinction of species dependent on others for their ecological niche—which Jared Diamond suggested in 1989 was one of the four horsemen of mass extinction (in his words, "overhunting, effects of introduced species, habitat destruction, and secondary ripple effects") [27]. Among the most obvious candidates for co-extinction are two main groups: pollinators (which can have a strict dependency on host plants) and endosymbionts (parasites and mutualists, which may exhibit strict specificity in their association with plant or animal hosts). While both groups are believed to be severely at risk of secondary extinction, quantifying their extinction rate can be challenging, as there is rarely a 1:1 correspondence between hosts and dependent species. An approach popularized by Koh simulates host extinctions in a random order and predicts the number of corresponding coextinctions from the *affiliation matrix*; by fitting a function to real affiliation matrices, Koh *et al.* found that if host specificity is 1:1 then the slope is linear, but when affiliates use a greater number of hosts, the coextinction function is concave upward,

$$\bar{A} = (0.35\bar{E} - 0.43)\bar{E}\ln\bar{s} + \bar{E}, \tag{1.6.1}$$

where E gives primary extinction risk, A secondary extinction risk, and s is host specificity [61]. Subsequent work has shown that even though parasites and mutualists may experience a reduced rate of extinction from host switching, the majority of threatened species on Earth might still be mutualists and parasites (due to the tremendous diversity of such species, e.g., the estimated 300,000 species of helminth alone [28]), and most of those extinctions are poorly cataloged [32]. More data is needed on host-symbiont association networks to better inform the role that nonrandom structure in those networks might play in increasing or decreasing extinction rates; some work has suggested that species preferentially favor more stable host species, the underlying cause of a "paradox of missing co-extinctions" [102]. Similarly, the potential for species to switch hosts and thereby avoid extinction is unknown, but likely mitigates global extinction risk. In parasitology, the Stockholm Paradigm suggests that host-parasite associations diversify in changing climates and environments as a function of (1) phenotypic plasticity, (2) trait integration and (3) phylogenetic conservatism of "latent potential" which together produce a pattern of *ecological fitting* that might benefit parasites (and thereby other symbionts) in the face of the sixth mass extinction [16]. A more in-depth treatment of the theoretical ecology of ecological fitting can be found in the recent work of Araujo *et al* [5].

Is saving microbes and parasites from extinction a reasonable goal? Some argue that it is [29], but others have recently suggested it's "time to get real about conservation" and focus on the fact we're not adequately preventing catastrophic population crashes in megafauna like elephants [34] or giraffes. Regardless of animal type or

conservation status, the development of demographic theory and predictive modeling are our best options to understand and mitigate extinction risk in natural populations. One such advance is the development of *early warning signals* of population collapse. This is a developing body of literature that is built around the fact that populations on the verge of collapse often produce detectable statistical signals [92]. If researchers are able to detect these signals in time series data before it is too late, mitigation efforts and prioritization of at-risk populations may prevent population collapse. Current work is attempting to scale the detection of early warning signals to the metapopulation level by developing spatial early warning signals [58], which could be used to optimize reserve design and address the influence of dispersal, stochasticity, and local population dynamics on metapopulation persistence.

The pressure for more accurate, predictive tools will only grow in the next few decades of research. A recent review by Mark Urban surveyed studies of climate change-driven extinction risk and found that, despite the variation between different modeling methods and scopes, projected extinction rates are not only rising but one in six species might be imminently threatened with extinction [105]. Similarly, in a study of roughly 1000 species of plants and animals, about half had experienced population extinctions driven by climate change [106]. As extinction rates accelerate due to global change and we fully enter the sixth mass extinction, the need for better analytical and simulation tools—that produce precise estimates from limited data—will only grow. In light of the constant need to test, revise and re-test models of extinction, to a mathematically trained ecologist or an ecologically-minded mathematician, this field of research is a critical opportunity to apply the principles of ecosystem science towards a high-impact and worthy goal.

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